SOME NEW GIVETIAN (LATE MIDDLE DEVONIAN) GASTROPODS FROM THE PAFFRATH AREA (BERGISCHES LAND, GERMANY)

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Frýda, J. 2000 06 30: Some new Givetian (late Middle Devonian) gastropods from the Paffrath area (Bergisches Land, Germany). *Memoirs of the Queensland Museum* **45**(2): 359-374. Brisbane, ISSN 0079-8835.

Revision of Givetian (Middle Devonian) gastropods from the Paffrath area (Bergisches Land, Germany) has identified a large number of new taxa described herein. These are Retispira tasselli sp. nov., Stenoloron (Paffratholoron) goldfussi subgen. et sp. nov., Quadricarina (Blodgettina) reticulata subgen. et sp. nov., Kirchneriella gen. nov., Eiserhardtia inepta gen. et sp. nov., Cerithioides whidbornei sp. nov., Plagiothyra multispiralis sp. nov., Naticopsis (Paffrathopsis) subgen. nov., Paffrathia lotzi gen. et sp. nov., Cookiloxa pulchra gen. et sp. nov., Palaeozygopleura (Rhenozyga) subgen. nov. and Heteroloxonema gen. nov.

Gastropods, Devonian, Givetian, Germany.

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During the last fifteen years the number of studies on Devonian gastropods has increased rapidly (e.g., Blodgett & Rohr, 1989; Blodgett, 1992, 1993; Blodgett & Johnson, 1992; Kase & Nishida, 1986, 1988; 11orný, 1992, 1994; Horný & lordan, 1993; Frýda, 1992, 1998c,d, 1999b; Frýda & Manda, 1997; Frýda & Bandel, 1997; Gubanov et al., 1995; Cook, 1993, 1997; Cook & Camilleri, 1997; Bandel & Frýda, 1998). Impetus for increased interest in this relatively neglected group of Devonian fossils were the seminal studies of Blodgett et al. (1988, 1990) who identified the great potential utility of Palaeozoic gastropods as paleobiogeographic indicators. In addition, research focused on the higher taxonomy of the Devonian gastropods, based on protoconch morphology, has shown that during Devonian time a large change-over occurred from a fauna of typical Early Palaeozoic cast, to one of a more modern aspect (see Frýda, 1999a and references therein). Revision of the Givetian (Middle Devonian) gastropods from Germany (Frýda, 1998a) have identified a large number of new taxa and revised material untouched for up to 150 years (Goldfuss, 1844). The results of this revision have only partially been published (Bandel & Frýda, 1998, 1999; Frýda, 1998b, 1999a) and the majority of them have been prepared for monographic publication. Because new taxonomic names established in an unpublished study (Frýda, 1998a) are prepared to be used in non-taxonomic studies by other authors, there is a problem with their priority as well as the fact that some of them would be nomina nuda. For this reason, some new Givetian (Middle Devonian) gastropods

from the Paffrath area (Bergisches Land, Germany) are established herein. Monographic treatment with detailed descriptions of all species belonging to newly established taxa as well as the evaluation of their palaeogeographical and stratigraphical distributions is in preparation (Frýda & Bandel, in prep.). All described gastropods come from the collection of Dr Volker Ebbighausen and are deposited in the Senckenberg Museum in Frankfurt au Main (Germany).

SYSTEMATIC PALAEONTOLOGY

AMPHIGASTROPODA Simroth, 1906 BELLEROPHONTOIDEA M'Coy, 1851 BELLEROPHONTIDAE M'Coy, 1851 KNIGHTITINAE Knight, 1956

Retispira Knight, 1945

TYPE SPECIES. Retispira bellireticulata Knight, 1945.

REMARKS. *Retispira* (Knight, 1945) is a complex genus within Knightitinae later regarded as a subgenus of *Knightites* Moore, 1941 (Knight et al., 1960). Batten (1972) suggested that *Retispira* represents a separate genus and this was followed by Gordon & Yochelson (1987). *Retispira* ranges from the Devonian to the Permian.

Retispira tasselli sp. nov. (Fig. 1F-J)

ETYMOLOGY. For the Australian paleontologist Chris Tassell.

MATERIAL. 6 specimens from Herrenstrunden, locality 9, Bergisches Land, Germany (coll. Ebbighausen). Holotype: figured herein as Fig. 1F,G

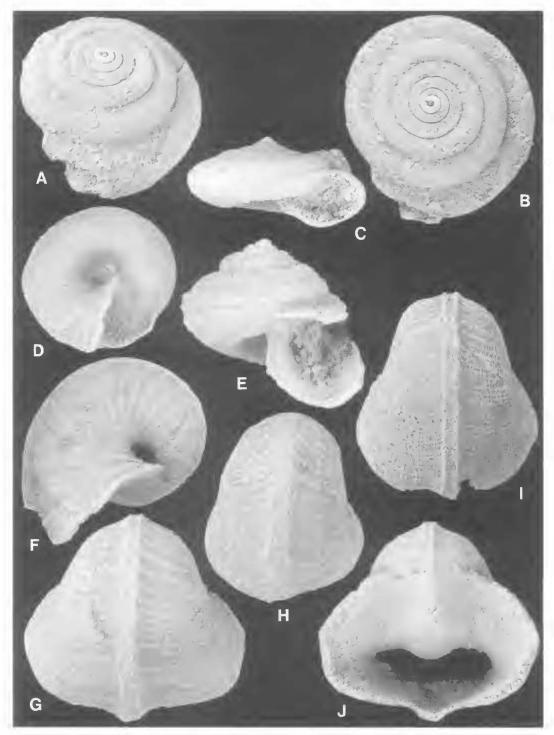


FIG. 1. A-C, Stenoloron (Paffratholoron) goldfussi sp. nov. A, Holotype, oblique view \times 3.5; B, Holotype, apical view \times 3.6; C, Paratype, apertural view \times 3.8. D, E, Quadricarina (Blodgettina) reticulata sp. nov. D, Holotype, basal view showing a reticular pattern \times 4; E, Holotype, apertural view \times 5. F-J, Retispira tasselli sp. nov. F, Holotype, lateral view showing a shell ornamentation \times 4.8; G, Holotype, dorsal view \times 4.8; H, Paratype A, dorsal view \times 7; I, Paratype B, dorsal view \times 4.5; J, Paratype C, apertural view \times 5.

TYPE LOCALITY. Bücheler Schichten, Middle Devonian (Givetian). Herrenstrunden, Bergisches Land, Germany.

DIAGNOSIS. Species of *Retispira* with small shell having a broad, flat selenizone raised above the shell dorsum; shell narrowly and deeply phaneromphalous; lateral portions of whorl profile rounded into narrow umbilici without any angulation; apertural lip of mature whorl is slightly expanded on its lateral and umbilical portions; shell ornament consisting of spiral and collabral lirae forming a reticulate pattern of longitudinally elongated rectangles.

DESCRIPTION. Small bellerophontid shell bearing a broad, flat selenizone raised above shell dorsum. Shell narrowly and deeply phancromphalous. Whorl profile slightly concave on each side of selenizone and gently convex in dorsolateral portions. Lateral portions of whorl profile curve into narrow umbilici without any angulation. Shallow and wide sinus in anterior margin of the outer lip culminates in a slit generating a raised selenizone. Selenizone bounded by two distinct spiral threads; width of the selenizone about 15% of width of shell dorsum. Apertural lip of the mature whorl slightly expanded on its lateral and umbilical portions. Shell ornament consists of spiral and collabral lirae; collabral lirae widely spaced and more expressed than closely spaced spiral lirae; spiral lirae crossing the collabral lirae form a reticulate pattern of longitudinally elongate rectangles. Distances of both spiral and collabral lirae vary considerably during the ontogeny.

REMARKS. Retispira tasselli resembles Retispira leda (Hall, 1861) from the Middle Devonian of North America in its similar whorl expansion in the adult whorl. However, R. tasselli sp. nov. differs by having a narrower shell, raised selenizone and by the absence of ornamentation of its selenizone. Bellerophon elegans de Ferussac & Orbigny, 1840 noted by Archiac & Verneuil (1842: 354, pl. 29, fig. 2) from the Paffrath region is similar to Retispira tasselli and most probably also belongs in *Retispira*. It is distinguished from the latter by the absence of a raised selenizone. Retispira tasselli is also similar to *Retispira* sp. of Blodgett (1992) from the Eifelian of Alaska, but may be distinguished by its more raised selenizone.

Rollins et al. (1971) discussed similarities of *Retispira* and *Bucanopsis* which have similar shell shapes. *Merriamites* Blodgett & Johnson, 1995 (=*Merriamella* Blodgett & Johnson, 1992.

previously occuppied homonym), based on the Middle Devonian species *Merriamites eurekae* from Nevada, is also similar to *Retispira* in having a reticulate ornamentation. *Merriamites* differs from *Bucanopsis*, the latter having an ornament of spiral threads, in having a much broader longitudinal keel on the inner floor of the whorl, a prominent reticulate pattern and a prominent, rounded parietal tooth. The presence of a keel on the inner floor of the whorl is a character by which *Bucanopsis* and *Merriamites* (both are placed in Carinaropsinae) differ from *Retispira*. Similarities in these genera with some Knightitinae were also noted by Blodgett & Johnson (1992).

ARCHAEOGASTROPODA Thiele, 1925 GOSSELETINIDAE Wenz, 1938

Stenoloron Oehlert & Oehlert, 1888 Stenoloron (Paffratholoron) subgen, nov.

TYPE SPECIES. Stenoloron (Paffratholoron) goldfussi sp. nov.

ETYMOLOGY. Paffratholoron, for the type locality.

DIAGNOSIS. Subgenus of *Stenoloron* Oehlert & Oehlert, 1888 having low spired, phaneromphalous shell with slowly expanding whorls.

REMARKS. Stenoloron (Paffratholoron) subgen, nov. has slowly expanding whorls. The distance of the upper suture from the shell periphery (measured in the apical view) is about 15% of its total shell width. This value is double (i.e. 30%) in the generic type species, *Stenoloron* viennavi (Oehlert & Oehlert, 1888). In addition, Devonian species of Stenoloron Oehlert & Oehlert, 1888, such as Stenoloron subaequitera (Chapman, 1916) from the Early Devonian of Australia, Stenoloron minor Blodgett & Johnson, 1992, from the Middle Devonian of North America, and Stenoloron pollens Perner, 1903 from the Early Devonian of Europe have similar values of whorl expansion as the type species (i.e. about 30%). For this reason the species described below is placed in a new subgenus.

Stenoloron (Paffratholoron) goldfussi sp. nov. (Fig. 1A-C)

ETYMOLOGY. For the German paleontologist August Goldfuss, who studied Devonian gastropods of the Paffrath area.

MATERIAL. 3 specimens from Unterthal, Paffrath area, Bergisches Land, Germany (coll. Ebbighausen). Holotype: figured herein as Fig. 1A,B.

TYPE LOCALITY. Unterer Plattenkalk, Middle Devonian (Givetian), Unterthal, locality 63, Bergisches Land, Germany.

DIAGNOSIS. As for subgenus.

DESCRIPTION. Small, turbiniform shell with a wide umbilicus, width about one quarter of total shell width. Width of shell having about 7 whorls measures about 15mm. Sides of shell slightly convex (i.e. cyrtoeonoid) due to decrease of the pleural angle in the last two whorls. Narrow, slightly convex selenizone situated high on the whorl bounded by a single shallow groove on the each side. Whorl profile above the selenizone rounded and nearly subhorizontal at the upper suture; sutures are shallow. Suture just below its selenizone in younger whorls; in the mature whorl, the distance of the lower groove bounding the selenizone and the lower suture is about one half of selenizone width. Shell surface smooth.

The initial portion of the shell is lost in the holotype but it is preserved in another specimen from the same locality figured herein as Fig. 1C. The high spired early whorls distinctly protrude above the upper, convex shell surface. During the further shell growth, the pleural angle continually increases, but in the last two whorls it again slightly decreases. For this reason the sides of the early shell are concave and slightly convex in the mature shell.

REMARKS. Stenoloron (Paffratholoron) goldfussi sp. nov. is the only species assigned to the subgenus. It is distinguished from the species of Stenoloron (Stenoloron) by shape of its manywhorled shell and characteristic slow expansion. The selenizone in *Stenoloron (Paffratholoron)* goldfussi sp. nov. is wider than in the generic type species Stenoloron (Stenoloron) viennayi and Stenoloron (Stenoloron) subaequitera (Chapman, 1916), but is simliar in width to Stenoloron (Stenoloron) minor Blodgett & Johnson, 1992. Stenoloron (Paffratholoron) goldfussi represents the youngest occurrence of the genus, previously reported from the Early Devonian and Silurian. The only other Middle Devonian species known is Stenoloron (Stenoloron) minor Blodgett & Johnson, 1992 from the Eifclian of central Nevada.

EOTOMARIIDAE Wenz, 1938

Quadricarina Blodgett & Johnson, 1992 Quadricarina (Blodgettina) subgen. nov.

TYPE SPECIES, Quadricarina (Blodgettina) reticulata sp. nov.

ETYMOLOGY. For the American paleontologist Robert B. Blodgett.

DIAGNOSIS. Similar to *Quadricarina* (*Quadricarina*), with low spired shell having distinctly raised selenizone above the whorl surface; shell ornament consisting of reticulate pattern.

REMARKS. Quadricarina Blodgett & Johnson, 1992 is represented by four Middle Devonian species. Three species, including its type species Quadricarina glabrobasis Blodgett & Johnson, 1992, come from the Eifelian of Nevada. Blodgett & Johnson (1992) also include Pleurotomaria lenticularis Goldfuss, 1844 from the Givetian of Germany. The turbiniform, phaneromphalous shells of Quadricarina species are characterised by a selenizone bordered by two pairs of revolving cords. A gently concave selenizone is situated at mid-whorl height. Shell ornament consists of fine collabral ribs. Quadricarina (Blodgettina) subgen. nov., is similar to hitherto known species of *Quadricarina* (Quadricarina) in general shell shape and the position of the selenizone, but differs in having a distinctly raised selenizone above the whorl surface and reticulate shell ornament.

Quadricarina (Blodgettina) reticulata sp. nov. (Fig. 1D,E)

ETYMOLOGY. In reference to the presence of reticulate ornamentation.

TYPE LOCALITY. U. Plattenkalk limestones, Middle Devonian (Givetian), Unterthal, locality 63, Bergisches Land, Germany.

MATERIAL. 10 specimens from Unterthal, locality 63, Bergisches Land, Germany (coll. Ebbighausen). Holotype: figured herein as Fig. 1D,E.

DIAGNOSIS. As for subgenus.

DESCRIPTION. Small, turbiniform shell with a selenizone situated at shell periphery. Mature spire consisting of about six whorls, width approximately I3mm. Outer lip of aperture forms a shallow sinus culminating in a peripheral carina that gives rise to a flat selenizone; selenizone distinctly protruding above whorl surface. Selenizone bordered by two pairs of revolving cords; outer pair forming its margin and inner pair spaced between outer cords. Inner cords always slightly thinner than the outer cords. Very narrow groove between the inner cords. Upper and lower whorl surfaces convex; sutures deep and impressed. Whorl profile below selenizone forms a rounded shell base with a deep, funnel-

like umbilicus. Width of umbilicus about one quarter of total shell width. Whorls embrace below the selenizone. Distance between lower margin of selenizone and lower suture greater than width of the flat, protruding selenizone. Shell ornament above and below spiral and collabral threads forming a reticulate pattern. About 25 spiral threads below the selenizone form small tubercles where they are crossed by collabral threads.

REMARKS. Quadricarina (Blodgettina) reticulata subgen. et sp. nov. may be distinguished from all species of Quadricarina (Quadricarina) by the presence of peripheral carina bearing a selenizone and by its reticulate ornamentation. However, it resembles Quadricarina sp. nov. B of Blodgett & Johnson (1992) in its low-spired shell, wide umbilicus and slightly raised, carinate periphery but differs by having the selenizone distinctly situated above the suture, and having reticulate ornament. Whorls embrace slightly above the selenizone in Quadricarina sp. nov. B. The carinate periphery suggests that the poorly known Quadricarina sp. nov. B may belong to Quadricarina (Blodgettina).

RAPHISTOMATIDAE Koken, 1896 OMOSPIRINAE Wenz, 1938

Kirchneriella gen. nov.

TYPE SPECIES. Turbo striatus Hisinger in Goldfuss, 1844.

ETYMOLOGY. For the German paleontologist Heinrich Sylvester Kirchner, who in 1915 published 'Mittel-devonische Gastropoden von Soetenich in der Eifel'.

DIAGNOSIS. Turbiniform, relatively low-spired shell with a very indistinct selenizone situated high on the whorls; lateral side of whorls rounded; shell ornament consisting only of spiral cords; spiral cords on the phaneromphalous shell base generally regularly spaced; more closely spaced than those on the upper whorl surface; a spiral cord is also present on the selenizone surface.

REMARKS. *Kirchneriella* gen. nov. closely resembles the Permian *Callistadia* Knight, 1945 in general shell shape, position of the indistinct selenizone and shell ornament. Carboniferous and Permian species of *Callistadia* may be distinguished from *Kirchneriella* gen. nov. by the shape of the lateral whorl profile which is rounded in *Kirchneriella*, but nearly vertical and straight or gently concave in *Callistadia* (see

Knight, 1945; Hoare & Sturgeon, 1978). Kirchneriella also shows some similarities with the type species of Gyroma Oehlert, 1888, Pleurotomaria baconnierensis (Ochlert, 1888), from the Lower Devonian of France, however this species has collabral and spiral ornaments, in contrast to Kirchneriella. Nevertheless, some Devonian species assigned to Gyroma, like the Frasnian Gyroma altaica (Verneuil, 1845) and Gyroma subcapillaria Vostokova, 1966, lack collabral ornament and probably belong to Kirchneriella. Blodgett (1992) noted the first occurrence of pre-Carboniferous Callistadia in Middle Devonian rocks (Eifelian of Alaska). Unfortunately, only two, poorly preserved specimens are known, preventing determination of whether they belong to *Callistadia* or to *Kirclmeriella*. The Middle Devonian 'Turbo' multistriatus Kirchner, 1915 and 'Turbo' aequistriatus Kirchner, 1915 may belong to Kirchneriella, but need to be restudied in detail. Kirchneriella striata (Hisinger in Goldfuss, 1844) is the only known species of this genus.

Family UNCERTAIN

Eiserhardtia gen. nov.

TYPE SPECIES. *Eiserhardtia inepta* sp. nov. by monotypy.

ETYMOLOGY. For the German paleontologist Klaus Eiserhardt for his kind help with SEM photos.

DIAGNOSIS. Discoidal shell having a very wide and flat selenizone which forms the whorl periphery; shell base phaneromphalous; width of umbilicus about one quarter of the shell width; selenizone of younger whorls is situated in distinct, U-shaped groove close to upper suture; upper suture forms abapical margin of the selenizone; shell ornamentation consisting of spiral and collabral elements forming a reticular pattern.

REMARKS. Eiserhardtia inepta sp. nov. is distinguished by its U-shape groove opening of the selenizone on the preceding whorl (Fig. 2G). In addition, the very wide and flat selenizone forming the whorl periphery is not common among Palaeozoic gastropods. Eiserhardtia resembles some Palaeozoic genera like the Ordovician Latitaenia Koken, 1925, Chepultapecia Ulrich in Weller & Clair, 1928, and Liospira Ulrich & Scofield, 1897 and the Devonian Umbotropis Perner, 1903 in general shell shape. However, the unusual subsutural groove easily differentiates it from all these genera.



FIG. 2. A-C, *Kirchneriella striata* (Hisinger in Goldfuss, 1844); A, apertural view × 4.5; B, basal view showing a spiral ornamentation, same shell as A, × 3.6; C, apical view × 5. D, *Cerithioides whidbornei* sp. nov., lateral view × 3.8. E-G, *Eiserhardtia inepta* sp. nov., Holotype; E, apical view showing shell ornamentation × 11; F, apertural view × 13; G, oblique view showing a subsutural groove × 13.

Eiserhardtia inepta sp. nov. (Fig. 2E-G)

ETYMOLOGY. Latin, ineptus, inept, unable.

MATERIAL. Only one complete shell, Unterthal, locality 63, Bergisches Land, Germany (coll. Ebbighausen). Holotype: figured herein as Fig. 2E-G.

TYPE LOCALITY. U. Plattenkalk limestones, Middle Devonian (Givetian), Unterthal, locality 63, Bergisches Land, Germany.

DIAGNOSIS. As for genus.

DESCRIPTION. Medium-sized, dextrally coiled, discoidal shell with a wide and flat selenizone situated at the shell periphery. Mature spire with about four whorls; width more than double its height. Outer lip of aperture forms a shallow sinus culminating at a peripheral selenizone. Selenizone parallel with shell axis and ornamented by irregularly spaced lunulae. Width of flat selenizone about one quarter of the whorl height. Outline of aperture elliptical with longer axis roughly perpendicular to shell axis. Whorl profile above sclenizone slightly convex, except close to the upper suture where it forms a U-shaped groove. Selenizone of younger whorls situated in this U-shaped groove (Fig. 2G); upper suture just below selenizone. Width of umbilicus about a quarter of the total shell width. Shell ornament consists of spiral and collabral threads forming a reticulate pattern. About 15 regularly spaced, spiral threads on the shell above the selenizone are crossed by backward curving collabral threads.

MURCHISONIIDAE Koken, 1896

Cerithioides Haughton, 1859

TYPE SPECIES. Cerithioides telescopium Haughton, 1859.

REMARKS. Cerithioides telescopium, was described from the Carboniferous of Ireland. Donald (1892) placed in its synonymy two additional Carboniferous species, Murchisonia maxima and Glyptobasis conica, both earlier described by de Koninck (1883). Batten (1966), who revised the type species of Cerithioides, expressed the opinion that Cerithioides conicus (de Koninck) is an independent species having Cerithioides maximus (de Koninck) as a junior synonym. He also agreed with Donald's placement of Murchisonia (Cerithioides?) oweni Donald, 1895 into Cerithioides and additionally placed Cerithioides? gleanensis Longstaff, 1926 into synonymy with this species. Batten (1966)

placed Murchisonia eversolensis Stauffer, 1909 from the Middle Devonian of Ohio into Cerithioides and considered it to be the earliest representative of the genus. Small shells of Cerithioides incomptum Linsley, 1968 from the Middle Devonian of the North America probably do not belong to Cerithioides. Cerithioides whidbornei sp. nov. has a similar whorl profile to C. eversolensis (Stauffer, 1909) and also lacks the spiral costae on shell base. Both species may belong to a new subgenus within Cerithioides using the latter characters differing them from the Carboniferous Cerithioides species.

Cerithioides whidbornei sp. nov. (Fig. 2D)

ETYMOLOGY. For the British paleontologist G.F. Whidborne who contributed much to our knowledge of the Devonian gastropods,

MATERIAL. 10 specimens from the type locality (coll. Ebbighausen). Holotype: figured herein as Fig. 2D.

TYPE LOCALITY. Middle Devonian (Givetian) limestones, Bergisch Gladbach, locality 65, Bergisches Land, Germany.

DIAGNOSIS. Species of *Cerithioides* lacking spiral costae on the shell base; wide selenizone situated in the middle of whorl.

DESCRIPTION. High-spired, dextrally coiled shell with almost straight sides. Whorl profile distinctly convex close to both upper and lower sutures and nearly flat or slightly concave at the mid-whorl. Suture moderately deep. Shell base rounded and anomphalous. Wide selenizone situated at mid-whorl with width about 20% of the distance between the lower and upper sutures. Outer apertural lip bears a wide sinus culminating in a wide slit. Margins of apertural sinus form an angle of about 90°. Inner lip covered by thin inductura. Ornamentation consists only of growth lines. Selenizone limited by a fine, spiral groove on each side and ornamented by irregularly spaced lunulae.

REMARKS. Cerithioides whidbornei sp. nov. may be distinguished from Cerithioides eversolensis by the position of the selenizone. In C. whidbornei, the wide selenizone is situated mid-whorl, however, in C. eversolensis (Stauffer, 1909) it is distinctly below mid-whorl. Its upper margin runs closely to mid-whorl and the distance between its lower margin and the lower suture is smaller than the width of the selenizone (see Stauffer, 1909, pl. 16, fig. 13). Cerithioides

whidbornei sp. nov. may be also distinguished from the type species *C. telescopium* Haughton, 1859, by the absence of spiral costae on its shell base. *Cerithioides oweni* Donald, 1895, differs from both Devonian species and the type species by its whorl profile which has a distinct angulation below the sclenizone (see Donald, 1895: pl. 10, figs 1, 1a).

NERITIMORPHA Golikov & Starobogatov, 1975

NERITOIDEA Rafinesque, 1815 PLAGIOTHYRIDAE Knight, 1956

Plagiothyra Whidborne, 1892

TYPE SPECIES. Monodonta purpurea Archiac & Verneuil, 1842.

REMARKS. Whidborne (1892) established Plagiothyra for species Monodonta purpurea Archiae & Verneuil, 1842 and his new species Plagiothyra archon Whidborne, 1892. The latter was described from the Middle Devonian of southwest England. Vostokova (1966) suggested a placement of the species Palaeotrochus praecursor Clarke, 1885 into Plagiothyra, but earlier Vostokova (1961) had established *Pseudoplagi*othyra for that species. Two new undescribed species of *Plagiothyra* occur in the Devonian of the North America (R.B. Blodgett, pers. comm.); one in the Eifelian age Cheeneetnuk Limestone of the west-central Alaska and a second species in the Emsian age Disappointment Bay Formation, Canadian Arctic Islands. The last species is the first Early Devonian occurrence, and thus the oldest representative of *Plagiothyra*.

Plagiothyra multispiralis sp. nov. (Fig. 3E-H)

ETYMOLOGY. *multispiralis*, referring to the shell ornamentation formed by many spiral threads.

MATERIAL. More than 30 specimens from the Unterthal, locality 63, Bergisches Land, Germany (coll. Ebbighausen). Holotype: figured herein as Fig. 3GH.

TYPE LOCALITY. U. Plattenkalk limestones, Middle Devonian (Givetian), Unterthal, locality 63, Bergisches Land, Germany.

DIAGNOSIS. Species of *Plagiothyra* ornamented by many spiral threads; plate-like ridge bearing a triangular tooth within aperture smaller than in type species.

DESCRIPTION. Dextrally coiled, turbiniform shell with a rapidly expanding whorls, shell height about 15mm. Shell base anomphalous,

sutures shallow and adpressed. Whorl profile shows distinctly stronger convexity near upper suture where it forms a small ramp. Whorls join the preceding whorl below its periphery. The margin of the outer apertural lip passes downward from the upper suture with strong backward obliquity, but without any curvature. Columellar lip covered by a thick inductura. Prominent, triangular tooth occurs on a very low platelike ridge in the middle of the parietal wall. Shell ornamentation consists of many spiral threads that may be crossed by fine growth lines. Number of spiral threads between the sutures is about 20. Threads more distinct on adapteal part of outer whorl surface.

REMARKS. *Plagiothyra multispiralis* sp. nov. differs from the type species, Plagiothyra purpurea Archiae & Verneuil, 1842, by having a lower-spired shell that is ornamented by many spiral threads. Shell ornamentation on Plagiothyra purpurea consists of several distinct rows of tubercles. The number of spiral elements between the sutures is about 20 in *Plagiothyra* multispiralis sp. nov., but only 8 in *Plagiothyra* purpurea. Shell ornament on P. multispiralis resembles that of the other two genera in the family Plagiothyridae, Dirachis Whidborne, 1891, and Littorinides Knight, 1937. However, shells of the Middle Devonian *Dirachis*, being ornamented by a lower number of more distinct spiral elements, bear two teeth in the aperture. The Carboniferous *Littorinides* has one low tooth on the columellar lip in contrast Plagiothyra multispiralis sp. nov. The similar shape of the apertural tooth and its position within the aperture, as well as the similar shell shape of P. purpurea and P. multispiralis, necessitate placement of the new species in the Plagiothyra.

NERITOPSIDAE Gray, 1847 NATICOPSINAE Miller, 1889

Naticopsis M'Coy, 1844 Naticopsis (Paffrathopsis) subgen. nov.

TYPE SPECIES. Natica subcostata Archiac & Verneuil, 1842.

ETYMOLOGY. For the type area, Paffrath, Germany.

DIAGNOSIS. *Naticopsis* having moderately low spired shells with strong collabral cords extending across entire whorl surface.

REMARKS. Yochelson (1953) placed *Natica* subcostata Archiac & Verneuil, 1842 into *Naticopsis (Jedria)* based on the Carboniferous

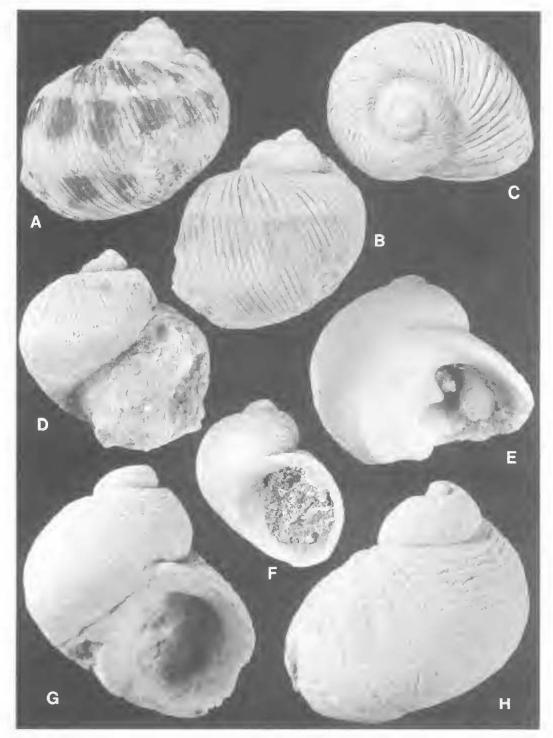


FIG. 3. A-D, *Naticopsis (Paffrathopsis) subcostata* (Archiac & Verneuil, 1842); A, abapertural view of shell with well preserved colour pattern × 3.3.; B, same shell covered with ammonium chloride × 3.3; C, apical view × 3; D, apertural view × 3. E-H, *Plagiothyra multispiralis* sp. nov.; E, Paratype A, apertural view showing a triangular tooth on low platelike ridge of the parietal wall × 7; F, Paratype B, apertural view × 3.5. G, Holotype, apertural view × 5; H, Holotype, abapertural view × 5.

Naticopsis meeki Knight, 1933. Naticopsis (Jedria) subcostata was the only Devonian species placed into Naticopsis (Jedria). Blodgett (1992) described Naticopsis (Jedria) deckeri from the Eifelian (Middle Devonian) of Alaska which is the oldest representative of this subgenus. Gordon & Yochelson (1987) noted that the body whorl extended downward rather than outward, and that the swelling on the outer whorl face above the periphery indicates the subgenus Jedria. All these shell characters may be seen in the Carboniferous species of *Naticopsis (Jedria)* as well as in *Naticopsis* (Jedria) deckeri, but not in Natica subcostata Archiae & Verneuil, 1842. N. subcostata has a moderately low spired shell with strong collabral cords extending across the entire whorl surface. These shell characters distinguish this species from all species included in *Naticopsis (Jedria)* as well as from other subgenera of *Naticopsis*. *Naticopsis* (*Paffrathopsis*) *subcostata* is the only species currently known.

Naticopsis (Paffrathopsis) subcostata (Archiac & Verneuil, 1842) (Fig. 3A-D)

non Buccinites subcostatus, Schlotheim1820: 130; Schlotheim 1822: 63, pl. 12, fig. 3.

Natica subcostata, 1842: 366, pl. 34, figs 5, 5a, 6; Goldfuss

1844: 116, pl. 198, fig. 22.

Turbonitella subcostata (Archiac & Verneuil) Lotz 1900: 212; Kirchner 1915 (partim): 238; Paeckelmann 1922: 41.

MATERIAL. Five complete shells and several fragments from the Unterthal, locality 63, and one complete shell from Bergisch Gladbach, locality 76, Bergisches Land, Germany (coll. Ebbighausen).

REMARKS. Goldfuss (1844) synonymised the species Buccinites subcostatus Schlotheim, 1820 and Natica subcostata Archiac & Verneuil, 1842. However, Schlotheim's figure (see Schlotheim, 1822, pl. 12, fig. 3) of Buccinites subcostatus differs from that of *Natica subcostata* (compare with Archiac & Verneuil, 1842, pl. 34, figs 5, 6). Material from Paffrath evidently belongs to the species Natica subcostata Archiac & Verneuil, 1842, which is the first unquestionable illustration of this species. For this reason, Archiac & Verneuil's name is considered to be a valid species

Colour Pattern. Traces of original colour pattern in Naticopsis (Paffrathopsis) subcostata (Archiac & Verneuil, 1842) were observed in specimens from Unterthal, locality 63, and Bergische Gladbach, locality 76. The geometry of the colour pattern in specimens from the both localities is the same. The colour pattern consists

of three spiral bands of black irregular spots (Fig. 3A). The distance between the spots in each band is about equal to their diameter. The whorl surface close to the upper suture is without any colour. Archiac & Verneuil (1842: pl. 34, figs 5, 6) and Roemer (1876: pl. 32, fig. 8) figured the same colour pattern as described herein in their figures of Natica subcostata (=Naticopsis (Paffrathopsis) subcostata).

Paffrathia gen. nov.

TYPE SPECIES. Paffrathia lotzi sp. nov.

ETYMOLOGY. For the type area, Paffrath, Germany.

DIAGNOSIS. Small, low spired turbiniform shell ornamented by strong, sharp collabral ribs extending across the entire whorl surface; shell wall very thick; whorl profile suboval.

REMARKS. Characteristic shell ornament consisting of the distinct collabral ribs (Fig. 4A, B) distinguishes *Paffrathia* from all Palaeozoic members of the family Neritopsidae. Absence of spiral elements and the presence of distinct collabral elements of the shell ornamentation have complicated the subfamily-level position of Paffrathia gen. nov. as well as Naticopsis (Paffrathopsis) subcostata (Archiac & Verneuil, 1842) within the Neritopsidae. According to Knight et al. (1960) the Naticopsinae unites shells without ornament (except for subsutural collabral threads or cords in some species). On the other hand, Palaeozoic members of the Neritopsinae are ornamented with pustules. Only the type species Paffrathia lotzi sp. nov. is known.

Paffrathia lotzi sp. nov. (Fig. 4A,B)

Turbonitella sp.?, Lotz, 1900: 213, pl. 3, fig. 8.

ETYMOLOGY. For H. Lotz who originally figured this species.

MATERIAL. One complete shell from the Unterthal, locality 63, Bergisches Land, Germany (coll. Ebbighausen). Holotype: figured herein as Fig. 4A,B.

TYPE LOCALITY. U. Plattenkalk limestones, Middle Devonian (Givetian), Unterthal, locality 63, Bergisches Land, Germany.

DIAGNOSIS. As for genus.

DESCRIPTION. Small, low spired turbiniform shells with at least four whorls. Whorl profile convexly arched. Height of the adult shell approximately equals width. Whorls embrace near base. Inner whorl profile suboval, sutures very deep. Whorl profile runs from the upper suture laterally for short distance to rounded spiral angulation, far from this angulation it curves downward forming convex lateral part of the whorl, and then continues across the rounded whorl base into deep umbilicus. Outer apertural lip is prosocline. Shell wall in adult whorl is relatively thick; about 20% of inner apertural diameter. Shell ornament consists of strong, sharp collabral ribs extending across the entire whorl surface. Ribs regularly spaced and their distance roughly equals half of the diameter of the aperture. Fine growth lines may be observed on the surface between collabral ribs.

REMARKS. *Paffrathia lotzi* is a rare element of gastropod fauna of the Givetian (Middle Devonian) U. Plattenkalk limestones of Germany, with the illustrated specimen (Fig. 4A,B) the only shell available for study. The specimen figured by Lotz (1900: pl. 3, fig. 8) seems to belong to this species. However, a larger collection of this species is needed for the study of shell variability.

? LOXONEMATOIDEA Koken, 1889

Cookiloxa gen. nov.

ETYMOLOGY. For the Australian paleontologist Alex Cook.

TYPE SPECIES. Cookiloxa pulchra sp. nov.

DIAGNOSIS. Slender, regular, high-spired and multiwhorled shell with straight sides having a gently convex whorl profile; sutures deep, whorls more arched close to both upper and lower sutures; external surface of whorls ornamented by collabral costae which are asymmetrically bent and crossed in the mid-whorl by one spiral costa.

REMARKS. Cookiloxa resembles Australoxa Cook & Camilleri, 1997 in its shell ornamentation. The latter genus is based on Australoxa tasselli Cook & Camilleri, 1997 from the Middle Devonian of Australia. The angular whorls of A. tasselli are ornamented by prominent opisthocline ribs and a low, sharp sinus is developed on the angular whorl periphery (see Cook & Camilleri, 1997: fig. 9E-L). One spiral cord occurs just above the lower suture. Cookiloxa gen. nov. differs from Australoxa in having a rounded whorl profile, a much smaller shell and by the absence of a peripheral sinus and lower spiral cord. Cookiloxa also resembles the Permian genera Loxosonia Batten, 1985 and Cibecuia

Winters, 1963 in shell ornament. Batten (1985) interpreted the spiral groove-like element of their shell ornamentation as a selenizone. Cookiloxa differs from Cibecuia by a different whorl profile, being distinctly convex in contrast to the latter genus which has a flat whorl profile. Cookiloxa has a similar whorl profile as both known species of Loxosonia, i.e. Loxosonia horrmotoma Batten, 1985 and Loxosonia zygo-pleuroides Batten, 1985. Cookiloxa may be distingushed from both species of *Loxosonia* by the position of its spiral element of shell ornamentation. In *Cookiloxa* costa-like spiral element is situated in the middle of the whorl, but in Loxosonia the groove-like spiral element (?= selenizone) occurs close to the upper suture. Cookiloxa also resembles the Ordovician genera Spiroecus Longstaff, 1924 and Donaldiella Cossmann, 1903. Spiroecus Longstaff, 1924, differs from Cookiloxa in having a more prominent spiral ornamental element being situated above the mid-whorl and forming a distinct angulation (see holotype in Knight, 1941: pl. 48, fig. 10). In addition S. girvanensis differs from Cookiloxa pulchra by the absence of collabral costae (but see specimen figured by Wenz, 1938: fig. 929b). *Cookiloxa* may be distinguished from the genus *Donaldiella* by its differing shape of the whorl profile and outer apertural lip. The Middle Devonian *Cookiloxa pulclira* sp. nov. from Germany is the only known species.

Cookiloxa pulchra sp. nov. (Fig. 4C,D)

ETYMOLOGY. Latin, pulcher, beautiful.

MATERIAL. About 30 specimens from the Herrenstrunden, Iocality 9, Bergisches Land, Germany (coll. Ebbighausen). Holotype: figured herein as Fig. 4D.

TYPE LOCALITY. Bücheler Schichten, Middle Devonian (Givetian), Herrenstrunden, locality 9, Bergisches Land, Germany.

DIAGNOSIS. As for genus.

DESCRIPTION. Small high-spired, dextrally coiled shell, up to 13 whorls present. Sides of shell nearly straight, whorl profile distinctly convex; maximum convexity close to both upper and lower sutures. Whorl profile nearly flat at mid-whorl. Sutures moderately deep. Lateral part of the whorl curves uniformly to base part, forming a smooth curvature without any angulation. Shell base rounded and anomphalous. Shell ornamentation consists of asymmetrically bent collabral costae being crossed in the mid-whorl

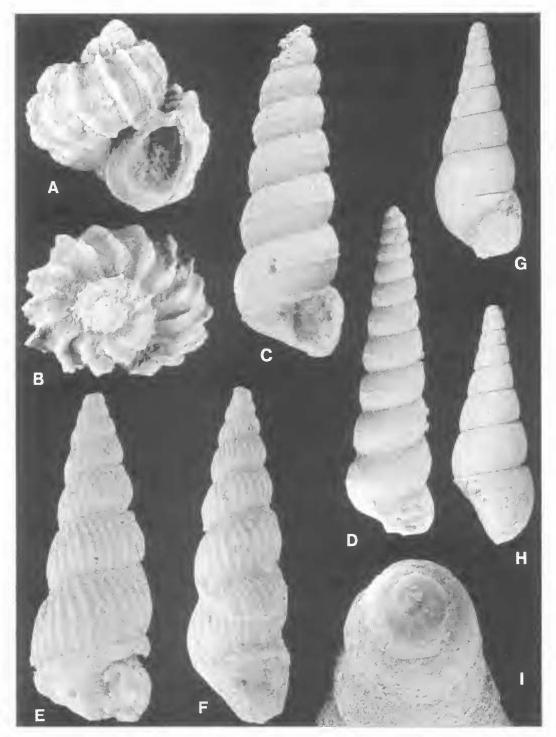


FIG. 4. A, B, *Paffrathia lotzi* sp. nov., Holotype; A, apertural view × 4.5; B, apical view × 4.5. C, D, *Cookiloxa pulchra* sp. nov.; C, Paratype A, lateral view × 14; D, Holotype, lateral view × 9. E, F, *Palaeozygopleura (Rheinozyga) retrostriatum* (Kirchner, 1915) comb. nov.; E, lateral view showing the regularly spaced orthocline costae × 15; F, lateral view of larger shell × 9. G-I, *Heteroloxonema moniliforme* (Goldfuss, 1842) comb. nov.; G, apertural view × 3.4; H, lateral view × 3.4; I, oblique view showing an early whorl × 125.

by one spiral costa. Beginning at the upper suture, the collabral costae run in prosocline direction, gradually curve in an orthocline direction, and then in opisthocline direction near the mid-whorl forming a wide, asymmetrical arched sinus.

REMARKS. Shape of the collabral costae in Cookiloxa pulchra sp. nov. resemble those of some species of Palaeozygopleura Horný, 1955 (i.e. the Early Devonian P. chhupaci Frýda, 1993, P. devonicans (Perner, 1907) and the Middle Devonian, P. hamiltonae (Hall, 1861)). Spiral costa in Cookiloxa pulchra is most probably just elements of the shell ornamentation and not a narrow selenizone. Without knowledge of the initial part of the shell Cookiloxa gen. nov. its higher taxonomic position remains questionable.

PALAEOZYGOPLEURIDAE Horný, 1955

Palaeozygopleura Horný, 1955 Palaeozygopleura (Rhenozyga) subgen. nov.

TYPE SPECIES. Loxonema retrostriatum Kirchner, 1915 (herein Fig. 4E,F).

ETYMOLOGY. Rhenozyga referring to Latin Rhemus, for the river Rhine.

DIAGNOSIS. Palueozygopleuro with orthocline or slightly opisthocyrt collabral costae; whorl between sutures strongly arched; shell cyrtoconoid or with straight sides.

REMARKS, Palaeozygopleura (Rhenozygu) subgen, nov, differs from all other subgenera of Palaeozygopleura by the shape of its collabral costae which are orthocline or slightly opisthocyrt. Palaeozygopleura (Rhenozyga) may be distinguished by its strongly arched whorls which are also higher than in all other subgenera of Palaeozygopleura. The orthocline or slightly opisthocyrt shape of costae resemble that of Devonozyga Horný, 1955. The whorls in Devonozyga Horný, 1955 are distinctly shouldered and in the median region flattened, in contrast to that in the Palaeozygopleura (Rhenozyga) subgen, nov. which has strongly arched whorl sides, Blodgett (1992) described a new genus Alaskozygopleura based on the Eifelian Alaskozygopleura crassicostata Blodgett, 1992 which he tentatively placed in the family Pseudozygopleuridae Knight, 1930. Palaeozygopleura (Rheinozyga) subgen. nov. resembles Alaskozygopleura in its shell ornamentation, but the former taxon may be distinguished from the latter its much narrower shell and circular

aperture. Blodgett (1992) noted broad variability of his Alaskozygopleura crassicostata, but all of the figured shells of his species have ovoid, adapically narrower apertures, considerably wider shells and higher whorls than Palaeozygopleura (Rhenozyga) retrostriatum (Kirchner, 1915).

Unfortunately there are no data about the early shell in the Givetian species of Palaeozygopleura (Rhenozyga) subgen, nov, All other subgenera of Palaeozygopleura have protoconchs of the archaeogastropod type (Frýda & Bandel, 1997). The placement of Rhenozyga in the genus Palaeozygopleura should be proved by type of its. protoconch. Besides the type species, Palaeozygopleura (Rhenozyga) retrostriatum (Kirchner, 1915), several other 'Loxonema' species from the Middle Devonian of Germany like Loxonemu spiraglobosum Kirchner, 1915 may belong to the new Palaeozygopleura (Rhenozyga). Palaeozygopleura machemyi Cook, 1997 from the Middle Devonian of Australia also is transferred to the new Palaeozygopleura (Rhenozyga). A detailed study of all Middle Devonian species resembling the genus Palaeozygopleura as well as comparison with the Eifelian Aluskozygopleura crassicostata Blodgett, 1992 is in preparation.

? HETEROSTROPHA Fischer, 1885

Heteroloxonema gen, nov.

TYPE SPECIES. Turritella moniliformis Goldfuss. 1844.

ETYMOLOGY. A combination of the generic name. Loxonema and the prefix hetero-because of the presumed heterostrophic coiling of its early shell.

DIAGNOSIS. Slender, high-spired and multiwhorled shell; first whorl planispirally or slightly sinistrally coiled; shell apex blunt and dome-like; teleoconch sides slightly convex; whorl profile gently convex between shallow, but with distinct sutures; teleconch surface smooth.

REMARKS. The smooth teleoconch of Hetero-loxonema gen. nov. resembles that of many loxonema gen. nov. resembles that of many loxonemaids including Loxonema, but may be distinguished by its dome-like shell apex formed by planispirally or slightly sinistrally coiled early whorl. All known Devonian loxonematoidean gastropods such as Katoptychia Perner, 1907, Stylonema Perner, 1907, Palaeozygopleura (Palaeozygopleura) Horný, 1955, Palaeozygopleura (Palaeozyga) Horný, 1955, and Palaeozygopleura (Bohemozyga) Frýda & Bandel, 1997 have an acute shell apex which is formed by the archaeogastropod-type protoconch. Heteroloxonema gen. nov. having a planispirally

or slightly sinistrally coiling of its early whorl may be distinguished by this character from all known loxonematoideans. This character distinguishes *Heteroloxonema* gen. nov. also from the genus *Donaldina* Knight, 1933, based on the Carboniferous Aclisina grantonensis Donald, 1898. According to Knight (1941), the latter species has 'earliest two whorls free from the spire, the first whorl planispirally coiled and tilted', in contrast to the blunt and dome-like shell apex of *Heteroloxonema*. In addition, the shells of the type species are ornamented by numerous spiral lirae (see Knight 1941: pl. 48, fig. 3a-e). Heteroloxonema moniliforme (Goldfuss, 1844) from the Middle Devonian of Germany is the only known species.

Heteroloxonema moniliforme (Goldfuss, 1844) (Fig. 4G-I)

Turritella moniliformis, Goldfuss 1844, p. 103, pl. 196, fig. 1. Loxonema moniliforma (Goldfuss), Bandel 1994, pl. 4, figs. 9-10.

Donaldina moniliforma (Goldfuss), Nützel,1997: 209, pl. 34 S-T.

MATERIAL. 13 complete shells from the Unterthal, locality 63, Paffrath area, Germany (coll. Ebbighausen).

DIAGNOSIS. As for genus.

DESCRIPTION. Medium sized, high-spired, dextrally coiled shells having at least 9 whorls. Shell sides slightly convex; sutural slope approximately 10°. The first whorl planispirally or slightly sinistrally coiled. Shell apex blunt and dome-like. Whorl profile gently convex and slightly flattened in median region; width of whorl almost twice of its height. Sutures are shallow but distinct. Shell base anomphalous, teleoconeh surface smooth.

REMARKS. Bandel (1994) figured the early whorl in *Heteroloxonema moniliforme* (Goldfuss, 1844) which is, according to his observation, sinistrally coiled. For this reason he considered it to be a member of the Heterostropha. If his interpretation is correct, then *Heteroloxonema moniliforme* represents the oldest known member of this subclass (Bandel, 1994) and also the only heterostrophid gastropod older than the Frasnian/Famennian mass extinction. Nevertheless, no protoconch/teleoconch boundary was hitherto observed in this species.

ACKNOWLEDGEMENTS

I thank Dr Volker Ebbighausen for providing material from his collection. This publication is

based on my studies of the Siluro-Devonian gastropods supervised by Klaus Bandel (Universität Hamburg), partly sponsored by the U.S.-Czechoslovak Science and Technology Joint Fund in cooperation with the Czech Geological Survey and U.S. Geological Survey under Project Number 95057. I gratefully thank Robert B. Blodgett (Oregon State University) and Alex G. Cook (Queensland Museum) for their useful critical remarks to the manuscript and improving its language.

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